



A Population Dynamic Model for Facultative Agamosperms

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Plants that can reproduce both sexually and agamically are called facultative apomicts. Some species, such as *Taraxacum*, contain both sexual diploids and triploid facultative apomicts. Triploids produce seeds without gamete fusion and recombination, and can also produce pollen and fertilize diploids. We present a population dynamic model that deals with gene flow and competition between diploids and triploids, with differing allocation towards reproductive investment in seeds and pollen. This paper examines whether diploids and triploids of plants with facultative agamospermy can coexist within a single population. We analyse the global behavior of such a dynamic system. Features of the system are significantly affected by the germination rates of diploids and triploids. Either diploids or triploids persist alone when the germination rate of diploids is sufficiently larger or smaller than that of triploids, respectively. Competitive exclusion occurs when both germination rates are sufficiently large. Coexistence is possible under certain specific conditions when: (I) the germination rates of both diploid sexuals and triploids are not sufficiently large, and (II) triploids produce sufficient pollen. When diploid sexuals and triploids coexist, triploids cannot exist alone, implying that the pollen of triploids is necessary to exploit diploid ovules.

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1. Introduction

Plants that can reproduce both sexually and agamically are called facultative apomicts. Some species, such as *Taraxacum*, include both triploid facultative apomicts and sexual diploids. Facultative apomicts form seeds without gamete fusion and recombination. Facultative apomixis is common in plants, and is found in about 15% of angiosperm plant families, although 75% of all apomicts belong to the Poaceae, Asteraceae, and Rosaceae families (Asker & Jerling, 1992). These

plants have polyploids and diploids, the former are facultative apomicts, while the latter reproduce sexually. Facultative apomicts also produce pollen and fertilize diploids in these plants. In *Taraxacum*, triploids produce haploid, diploid, or triploid pollen that fertilizes diploids, enabling diploids to produce diploid and triploid seeds (Richards, 1986; Morita *et al.*, 1990a).

Several articles have reported the geographic distributions of polyploids and diploids within a single species. Empirical studies suggest that diploid and polyploid types of *Eupatorium* (Compositae) are geographically separated (Sullivan, 1976; Kawahara *et al.*, 1989). On the other hand, diploids and polyploids coexist within

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populations of *Taraxacum* (Compositae) (Den Nijs *et al.*, 1990), *Antennaria* (Anteraceae) (Bayer *et al.*, 1991) and *Amelanchier* (Rosaceae) (Campbell & Dickinson, 1990). Den Nijs & Sterk (1984) showed that *Taraxacum* populations may be pure triploid, pure diploid, or mixed. Thus, the ratio of diploids to polyploids varies among populations. The ecological situation that brings about the coexistence of polyploids and diploids is unknown.

Models of competition between asexual and sexual strains within a single population have been used to explain the evolution and maintenance of sexual reproduction. Asexual strains probably invade sexual populations due to the two-fold advantage of sex (Williams, 1975; Maynard Smith, 1978). Recent models show how a small competitive advantage for sex can cancel the growth advantage resulting from asexuality in a density-dependent system (Doncaster *et al.*, 2000; Kerszberg, 2000). Most models of competition between sexual and asexual types assume that asexuality is obligate, and that no genes are exchanged between the two types. However, gene flow does exist between polyploids and diploids in plants with facultative agamospermy. In this paper, we present a mathematical model that deals with facultative agamospermy and includes gene flow between diploids and triploids, such as exists in dandelions. We examine whether diploid sexuals and triploid apomicts can coexist within a single population.

We focus on the allocation of reproductive investment in pollen and seeds. For simplicity, we assume that a plant is monocarpic, unlike dandelions. We analyse the stability properties of pure diploids, pure apomicts, and mixed populations, and discuss the conditions under which a stable equilibrium is possible. Although the germination rate may change with environmental conditions and the accumulation of deleterious mutations over the long term, we consider a constant environment and ignore genetic degradation of asexual strains, and discuss the short term.

2. Model

Our model is based on a monocarpic annual plant population that consists of sexual diploids

and facultatively apomictic triploids. Diploids produce haploid pollen and ovules via meiosis in the usual fashion. However, triploids produce both haploid and diploid pollen via meiosis and triploid ovules via agamospermy. Agamospermous triploids of *Taraxacum* form male gametes with haploid, diploid, or triploid chromosome sets, although most gametes have incomplete sets and die (Richards, 1973). For simplicity, we ignore triploid pollen in our model. We assume that triploids produce haploid pollen with probability r and diploid pollen with probability $1 - r$. Diploid seed is produced when haploid pollen fertilizes a haploid ovule. Triploid seed is produced either (1) when diploid pollen fertilizes a haploid ovule or (2) when a triploid ovule becomes a seed without pollination. The system of reproduction is summarized in Fig. 1. We describe the diploid and triploid population densities at generation t by x_t and y_t , respectively. We assumed that a diploid individual produces a pollen grains and that an apomict individual produces b pollen grains. Therefore, an apomict individual produces rb haploid pollen and

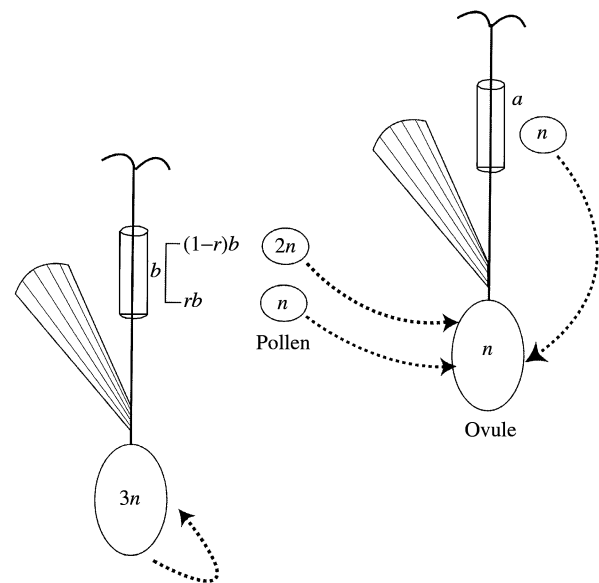


FIG. 1. Mating scheme used in our model with hybridization between diploids and apomicts. All facultative apomicts are apomictic and all diploids are sexual. Apomicts (left) not only cross with diploids (right), but also reproduce without pollination. A diploid individual produces a haploid pollen grains. An apomictic individual produces b both haploid and diploid pollen grains with probability r and $1 - r$, respectively.

$(1 - r)b$ diploid grains. We assumed that haploid ovules from diploid donors randomly cross with pollen from diploids and triploids. In intermixed populations consisting of diploids and triploids, the total number of pollen grains at generation t is $ax_t + by_t$. Assuming random mating within the population, the probability that haploid ovules produced by diploids are fertilized by haploid pollen from diploid donors is given by $ax_t/(ax_t + by_t)$. On the other hand, the probability of crossing a haploid ovule produced by diploids and diploid pollen from triploid donors is given by $(1 - r)by_t/(ax_t + by_t)$. This cross produces a triploid seed. In the same way, the probability of crossing a haploid ovule produced by a diploid and haploid pollen from a triploid donor is given by $rby_t/(ax_t + by_t)$. This cross produces a diploid seed.

We consider the cost of sexuality and impose restrictions on sexual compensation. Both diploids and triploids have limited resources available to produce pollen and ovules. Let K_1 and K_2 denote the weight of total reproductive investment per diploid and triploid, respectively. The weight of a pollen grain from diploid donors is k_1 and that from triploid donors is k_2 . A diploid invests k_1a in pollen and $K_1 - k_1a$ in seeds, while a triploid produces the weight of $K_2 - k_2b$ seeds. We define g_1 and g_2 as the germination rate of diploids and triploids, respectively. Let g_3 be the germination rate of hybrid diploid seeds, and g_4 be the germination rate of hybrid triploid seeds. The germination rate of seeds may depend on seed size or ploidy. Note that $K_1 - k_1a$ and $K_2 - k_2b$ must not be negative.

The population dynamics of diploids x_t and triploids y_t is given as follows:

$$x_{t+1} = \left[g_1(K_1 - k_1a) \frac{ax_t}{ax_t + by_t} x_t + g_3(K_1 - k_1a) \frac{rby_t}{ax_t + by_t} x_t \right] F_1, \quad (1)$$

$$y_{t+1} = \left[g_2(K_2 - k_2b)y_t + g_4(K_1 - k_1a) \frac{(1 - r)by_t}{ax_t + by_t} x_t \right] F_2, \quad (2)$$

where F_1 and F_2 are the rates at which diploids and triploids survive and reach maturity (to produce the next generation), respectively.

Within a population, there is competition for resources, such as light and nutrients, while germinated seeds develop to the adult stage. We assume that competition specifically occurs among seedlings. F_1 and F_2 were assumed to depend on total densities within a population. Let z_t be the total density of seedlings produced at generation t , defined as

$$z_t = \frac{(K_1 - k_1a)x_t}{ax_t + by_t} \{g_1ax_t + g_3rby_t + g_4(1 - r)by_t\} + g_2(K_2 - k_2b)y_t. \quad (3)$$

We assume that the survival probabilities F_1 and F_2 monotonically decrease and approach 0 as the total seed population density z_t increases:

$$F_i(z_t) = \varepsilon_i e^{-\rho_i z_t} (\leq \varepsilon_i) \quad (i = 1, 2), \quad (4)$$

where ε_i , the maximal survival probability, and ρ_i , the coefficient of density effect, are positive constants (Ricker, 1954). Assuming that the coefficient of density effect of diploids is equal to that for triploids, then $\rho_1 = \rho_2 = \rho$. If the functional form of density dependence follows Michaelis-Menten [$F_i(z) = \varepsilon_i z / (m + z)$], the stability property becomes simpler. The necessary conditions for coexistence can be demonstrated even when we use eqn (4) and the equilibrium is unstable.

From eqns (1-4), we constructed the following mathematical model:

$$x_{t+1} = \left\{ \alpha(s_1 - a) \frac{ax_t^2}{ax_t + by_t} + \delta(s_1 - a) \frac{rbx_t y_t}{ax_t + by_t} \right\} e^{-\rho z_t}, \quad (5)$$

$$y_{t+1} = \left\{ \gamma(s_2 - b)y_t + \beta(s_1 - a) \frac{(1 - r)bx_t y_t}{ax_t + by_t} \right\} e^{-\rho z_t}, \quad (6)$$

$$z_t = \frac{(s_1 - a)x_t}{ax_t + by_t} \left\{ \frac{\alpha ax_t}{\varepsilon_1} + \frac{\beta(1-r)by_t}{\varepsilon_2} + \frac{\delta rby_t}{\varepsilon_1} \right\} + \frac{\gamma(s_2 - b)y_t}{\varepsilon_2}, \tag{7}$$

where $\alpha \equiv \varepsilon_1 g_1 k_1$, $\beta \equiv \varepsilon_2 g_4 k_1$, $\gamma \equiv \varepsilon_2 g_2 k_2$, $\delta \equiv \varepsilon_1 g_3 k_1$, $K_1/k_1 \equiv s_1$, $K_2/k_2 \equiv s_2$, $s_1 > a$ and $s_2 > b$.

3. Analysis

3.1. DENSITY RATIO ψ_t

Let the density ratio $\psi_t \equiv x_t/y_t$. In this section, we consider the case $y_t > 0$. We obtain the following one-dimensional discrete dynamic system for ψ_t , from eqns (5-7):

$$\psi_{t+1} = \frac{(s_1 - a)(\alpha\alpha\psi_t + rb\delta)\psi_t}{\{\beta b(1-r)(s_1 - a) + a\gamma(s_2 - b)\}\psi_t + b\gamma(s_2 - b)} \equiv f(\psi_t). \tag{8}$$

$f(\psi_t)$ is the monotonically increasing function of ψ_t , independent of z_t . Let ψ^* be the non-trivial equilibrium satisfying $\psi^* = f(\psi^*) > 0$, which is explicitly and uniquely obtained as

$$\psi^* = \frac{b\{\gamma(s_2 - b) - r\delta(s_1 - a)\}}{a\{\alpha(s_1 - a) - \gamma(s_2 - b)\} - \beta b(1-r)(s_1 - a)}. \tag{9}$$

Since $s_1 > a$ and $s_2 > b$, a positive equilibrium ψ^* exists if and only if

$$l_1 < \gamma < l_2 \tag{10}$$

or

$$l_2 < \gamma < l_1, \tag{11}$$

where l_1 and l_2 are defined by

$$l_1 = \frac{s_1 - a}{s_2 - b} \left\{ \alpha - \frac{b\beta(1-r)}{a} \right\}, \tag{12}$$

$$l_2 = \frac{r(s_1 - a)}{s_2 - b} \delta. \tag{13}$$

If eqn (10) is satisfied, a positive equilibrium ψ^* given by eqn (9) is globally stable. Therefore, $f(\psi)/\psi > 1$ if $\psi < \psi^*$ and $f(\psi)/\psi < 1$ if $\psi > \psi^*$ [Fig. 2(a)].

In contrast, if eqn (11) is satisfied, the positive equilibrium ψ^* is always unstable, whereas the zero equilibrium is locally stable, because $f(\psi)/\psi < 1$ if $\psi < \psi^*$ and $f(\psi)/\psi > 1$ if $\psi > \psi^*$ [Fig. 2(b)]. The cobweb method (Mooney & Swift, 1999) clearly shows that if the initial value ψ_0 is less than ψ^* , ψ_t monotonically decreases over generations (iterations) and asymptotically approaches 0. On the other hand, if ψ_0 is greater than ψ^* , ψ_t monotonically increases to positive infinity. Thus, whether ψ_t converges to 0 or diverges to $+\infty$ depends on the initial conditions. The given system has a bistable structure.

From these arguments, if $f'(0) < 1$ is satisfied, but eqn (10) is not, then the value of $f(\psi)$ must always be less than ψ for any positive ψ . Therefore, the cobweb method shows that $\psi_t \rightarrow 0$ as

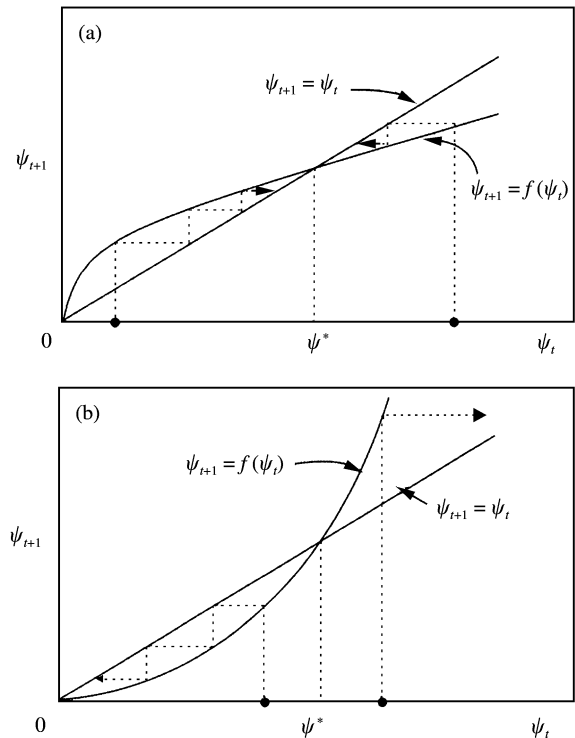


FIG. 2. The graph of function $f(\psi)$ given by eqn (8) is shown by a solid curve. The broken line shows the iterating trajectory of eqn (8): (a) ψ_t approaches a positive equilibrium, and (b) approaches 0 or diverges to $+\infty$. The initial condition is indicated by the dot on the ψ_t -axis.

$t \rightarrow +\infty$ for any positive initial value ψ_0 . The necessary and sufficient condition for $f'(0) < 1$ is

$$\gamma > l_1, l_2. \tag{14}$$

Similarly, if $f'(0) > 1$ is satisfied, but eqn (11) is not, then the value of $f(\psi)$ must always be greater than ψ for any positive ψ . Therefore, the cobweb method indicates that $\psi_t \rightarrow +\infty$ as $t \rightarrow +\infty$ for any positive initial value ψ_0 . The necessary and sufficient condition for $f'(0) > 1$ is

$$\gamma < l_1, l_2. \tag{15}$$

3.2. ASYMPTOTIC BEHAVIOR OF x_t AND y_t

We focus on the dynamic property of the ratio ψ . In this section, we consider the dynamic properties of densities x_t and y_t for the following separate instances: (I) $\psi_t \rightarrow 0$, (II) $\psi_t \rightarrow +\infty$, and (III) $\psi_t \rightarrow \psi^*$. From eqns (5–7), x_t and y_t do not positively diverge (see below). In each case, the absolute density may either approach 0, approach a unique finite-positive equilibrium or fluctuate permanently. Since the germination rate is assumed to depend on seed size, seeds originating from the ovules of diploids should have the same germination rate, regardless of ploidy. Thus, $g_1 = g_3 = g_4$ and $\alpha \equiv \delta$. A discrete dynamic system (5–7) has four equilibria, described as $(0, 0)$, $(0, \tilde{y})$, $(\tilde{x}, 0)$, and (\hat{x}, \hat{y}) . System (5–7) may not reach equilibrium. If $\psi_t (\equiv x_t/y_t)$ reaches 0, then x_t reaches 0 and y_t reaches 0 or is kept positive. If $\psi_t \rightarrow \psi^*$, given by eqn (9), x_t and y_t either simultaneously reach 0 or both remain positive. If $\psi_t \rightarrow +\infty$, (x_t, y_t) becomes either $(0, 0)$ or $(\tilde{x}, 0)$, and thus y_t reaches 0 and x_t reaches 0 or is kept positive. We investigate (I) the dynamical behavior of y_t if $x_t \equiv 0$, (II) that of x_t if $y_t \equiv 0$, and (III) that of x_t , if $y_t \equiv x_t/\psi^*$.

3.2.1. Dynamic Behavior of Apomictic Triploids

We consider the condition $x_t \equiv 0$. From eqns (6) and (7), we obtain

$$y_{t+1} = \gamma(s_2 - b)y_t e^{-\rho\gamma(s_2 - b)y_t/\varepsilon_2} \equiv f_1(y_t). \tag{16}$$

Since eqn (16) indicates a Ricker type of discrete dynamic system, y_t does not positively diverge. When eqn (14) is satisfied, equilibrium $(0, 0)$ is

stable if and only if, $f'_1(0) < 1$, i.e. $\gamma(s_2 - b) < 1$. Under this condition, y_t converges to 0 for all $y_0 > 0$. The non-trivial equilibrium satisfies $f_1(\tilde{y}) = \tilde{y}$. From eqn (16), we can easily obtain the unique equilibrium $\tilde{y} = \varepsilon_2 \ln[\gamma(s_2 - b)]/\rho\gamma(s_2 - b)$. The equilibrium \tilde{y} exists if $\gamma(s_2 - b) > 1$. \tilde{y} is globally stable if $|f'_1(\tilde{y})| = |1 - \ln[\gamma(s_2 - b)]| < 1$, or if $0 < \ln[\gamma(s_2 - b)] < 2$. Therefore, \tilde{y} exists and is stable if

$$1 < \gamma(s_2 - b) < e^2. \tag{17}$$

In contrast, the equilibrium \tilde{y} exists and is unstable if $\gamma(s_2 - b) > e^2$. Figure 3 shows the following asymptotic behaviors for the number of triploids: triploid apomicts (Ia) become extinct, (Ib) reaches a positive equilibrium, or (Ic) persist and fluctuate permanently.

3.2.2. Dynamic Behavior of Diploids

Next, we consider the condition $y_t \equiv 0$. From eqns (5) and (7), we obtain

$$x_{t+1} = \alpha(s_1 - a)x_t e^{-\rho\alpha(s_1 - a)x_t/\varepsilon_1} \equiv f_2(x_t). \tag{18}$$

Since $f_2(x_t)$ also indicates a Ricker type of discrete dynamic system, x_t does not positively diverge

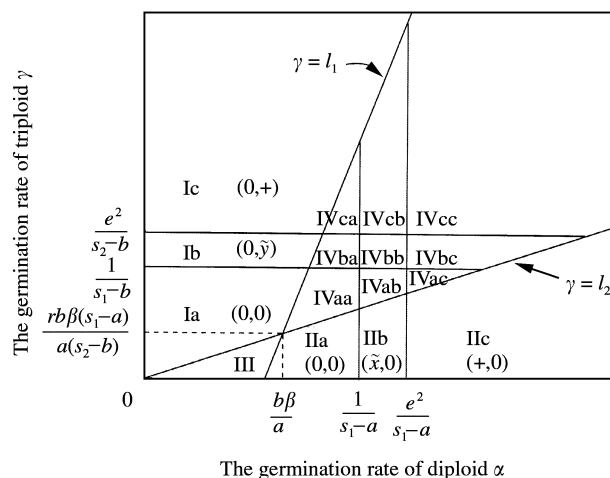


FIG. 3. Dynamic behavior of x_t and y_t , where $\psi_t \rightarrow 0$ (Domain I), $\psi_t \rightarrow \infty$ (Domain II), $\psi_t \rightarrow \psi^*$ (Domain III), and $\psi_t \rightarrow 0$ or $\psi_t \rightarrow +\infty$ depending on the initial relative density (Domain IV) for the case where $b\beta/\alpha < 1/(s_2 - a)$ and $rb\beta(s_1 - a)/a < 1$. The fitness of an apomict (γ) plotted against that of a diploid (α). Diploids become extinct in Domain I and apomicts in Domain II. See the text for subcategories (a)–(c) in Sections 3.2.1 and 3.2.2. See Fig. 5 for subcategories (a)–(c) in Domain III.

either. When eqn (15) is satisfied, equilibrium (0, 0) is stable if $f'_2(0) < 1$, i.e. $\alpha(s_1 - a) < 1$. Under this condition, x_t converges to 0 for all $x_0 > 0$. The non-trivial equilibrium satisfies $f_2(\tilde{x}) = \tilde{x}$. From eqn (18), we can easily obtain the unique equilibrium $\tilde{x} = \varepsilon_1 \ln[\alpha(s_1 - a)]/\rho\alpha(s_1 - a)$. As used to obtain condition (17), the equilibrium \tilde{x} exists and is globally stable if

$$1 < \alpha(s_1 - a) < e^2. \quad (19)$$

In contrast, the equilibrium \tilde{x} exists and is unstable if $\alpha(s_1 - a) > e^2$. Domain II in Fig. 3 shows the following types of asymptotic behaviors for diploids: diploids (IIa) become extinct, (IIb) reach positive equilibrium, or (IIc) persist and fluctuate permanently.

3.2.3. Asymptotic State of Coexistence

We consider what happens when $x_t \equiv y_t\psi^*$ with ψ^* given by eqn (9). From eqns (5–7),

$$x_{t+1} = \alpha(s_1 - a) \frac{ax_t + rby_t}{ax_t + by_t} x_t e^{-\rho z_t} < z_t e^{-\rho z_t} \\ \forall x_t, \forall y_t > 0, \quad (20)$$

$$y_{t+1} = \left\{ \beta(s_1 - a) \frac{(1-r)bx_t}{ax_t + by_t} + \gamma(s_2 - b) \right\} \\ \times y_t e^{-\rho z_t} < z_t e^{-\rho z_t} \quad \forall x_t, \forall y_t > 0. \quad (21)$$

$ze^{-\rho z}$ maximizes $1/\rho e$ at $z = 1/\rho$. Therefore, both x_t and y_t do not positively diverge. Since ψ_t monotonically approaches ψ^* irrespective of x_t and y_t as shown by (a) in Fig. 2, we expect $x_t \rightarrow y_t\psi^*$ and consider the asymptotic dynamics of x_t after $x_t \equiv y_t\psi^*$. Substitution of y_t by x_t/ψ^* into eqns (5–7) leads to

$$x_{t+1} = \alpha(s_1 - a) \frac{(a\psi^* + rb)}{a\psi^* + b} x_t e^{-\rho z_t} \quad (22)$$

and

$$x_{t+1} = \left\{ \beta(s_1 - a) \frac{(1-r)b\psi^*}{a\psi^* + b} + \gamma(s_2 - b) \right\} x_t e^{-\rho z_t}, \quad (23)$$

respectively. Simplifying, eqns (22) and (23) become

$$x_{t+1} = Ax_t e^{-2\rho Ax_t} \equiv g(x_t), \quad (24)$$

where

$$A = \alpha(s_1 - a) \frac{(a\psi^* + rb)}{a\psi^* + b} \\ = \beta(s_1 - a) \frac{(1-r)b\psi^*}{a\psi^* + b} + \gamma(s_2 - b).$$

From eqn (9), A becomes

$$A = \alpha \frac{a\gamma(s_2 - b) - rb\beta(s_1 - a)}{a\alpha - b\beta}. \quad (25)$$

A is positive if eqn (10) is satisfied. Quantity A determines the stability property of this system. We consider the non-trivial unique equilibrium \hat{x} satisfying $\hat{x} = g(\hat{x})$ for the one-dimensional discrete dynamic system (24), and obtain

$$\hat{x} = \frac{\log A}{2\rho A}. \quad (26)$$

The function $g(x)$ is positive and finite for all $x \geq 0$ and reaches a maximum at $x = 1/(2\rho A)$. Therefore, x_t never positively diverges. When ψ^* is stable, the dynamic behavior of x_t has three cases determined by A : (IIIa) $A < 1$, (IIIb) $1 < A < e^2$, and (IIIc) $A > e^2$. In case (IIIa), x_t and y_t ($\equiv \psi^*/x_t$) converge to 0 for all $x_0 > 0$ if $A < 1$, i.e. $\gamma > \max(\gamma_1, l_1)$, where

$$\gamma_1 = \frac{a + rb(s_1 - a)\beta}{a(s_2 - b)} - \frac{b\beta}{a(s_2 - b)\alpha}. \quad (27)$$

In case (IIIb), x_t converges to the positive equilibrium \hat{x} if $1 < A < e^2$, i.e. $\max(\gamma_2, l_1) < \gamma < \min(\gamma_1, l_2)$, where

$$\gamma_2 = \frac{ae^2 + rb(s_1 - a)\beta}{a(s_2 - b)} - \frac{e^2 b\beta}{a(s_2 - b)\alpha}. \quad (28)$$

Finally, in case (IIIc), diploids and apomicts coexist with cyclic or chaotic fluctuations if $A > e^2$, i.e. $l_1 < \gamma < \min(\gamma_2, l_2)$. The hatched region in Fig. 4 represents a globally stable coexisting

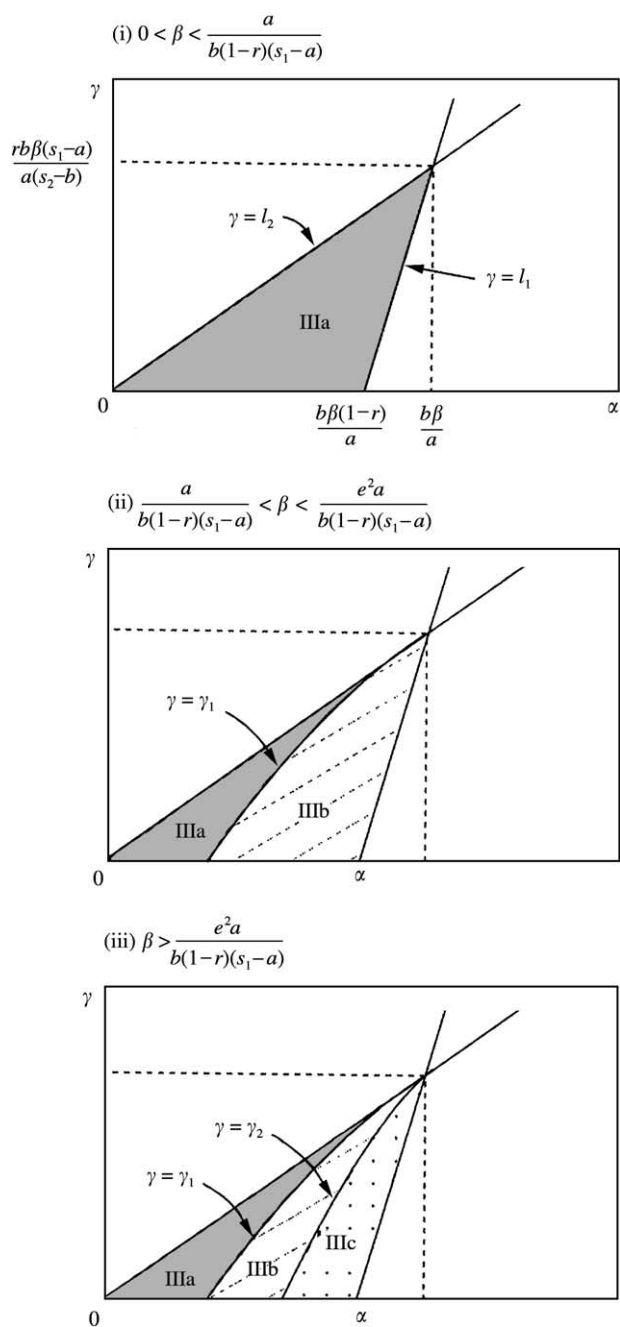


FIG. 4. Stability property for (i) $0 < \beta < a/b(1-r)(s_1 - a)$, (ii) $a/b(1-r)(s_1 - a) < \beta < e^2 a/b(1-r)(s_1 - a)$ and (iii) $\beta > e^2 a/b(1-r)(s_1 - a)$. Both diploids and apomicts become extinct in Domain (IIIa). Diploids and apomicts coexist in Domain (IIIb). Domain (IIIc) shows that both diploids and apomicts persist and fluctuate stably.

equilibrium (\hat{x}, \hat{y}) , where $\hat{y} = \hat{x}/\psi^*$. The dotted region in Fig. 4 represents persistent, but fluctuating, levels of diploids and apomicts. We investigate the dynamic behavior of x_t numerically. After 10 000 generations, the system reaches

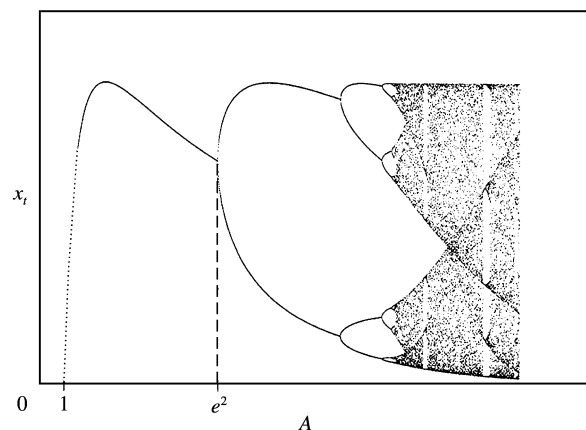


FIG. 5. Attractors for eqn (24) when $\rho = 1$ and $x_0 = 100$. For $0 < A < 1$, x_t converges to 0. For $1 < A < e^2$, equilibrium \hat{x} is locally stable. For $A > e^2$, equilibrium \hat{x} becomes unstable and periodic cycles appear as A increases.

periodic or chaotic oscillations. Figure 5 shows the population for the last 100 generations. Simulations starting from a population size of 100 reveal a bifurcation diagram of x_t . \hat{x} becomes unstable and the system has periodic cycles as A increases. Increasing A further results in periodic doubling in the asymptotic state and finally results in a chaotic state.

When $\psi_t \rightarrow 0$ (Domain I in Fig. 3), y_t has three asymptotic states: $(x_t, y_t) \rightarrow (0, 0)$, $(0, \hat{y})$, $(0, \text{variable})$. The asymptotic state \hat{y} depends on γ if $\psi_t \rightarrow 0$. When $\psi_t \rightarrow +\infty$ (Domain II in Fig. 3), x_t has three asymptotic states: $(x_t, y_t) \rightarrow (0, 0)$, $(\tilde{x}, 0)$, $(\text{variable}, 0)$. The asymptotic state \tilde{x} depends on α if $\psi \rightarrow +\infty$. When $\psi \rightarrow \psi^*$ (Domain III in Fig. 4), (x_t, y_t) has asymptotic states: $(x_t, y_t) \rightarrow (0, 0)$, (\hat{x}, \hat{y}) , $(\text{variable}, \text{variable})$. The asymptotic state (\hat{x}, \hat{y}) depends on A if $\psi \rightarrow \psi^*$. When the fate of ψ_t depends on the initial value (Domain IV in Fig. 3), nine asymptotic states arise: (IVaa) $(0, 0)$ (not bistable), (IVab) $(\tilde{x}, 0)$ or $(0, 0)$, (IVac) $(\text{variable}, 0)$ or $(0, 0)$, (IVba) $(0, 0)$ or $(0, \hat{y})$, (IVbb) $(\tilde{x}, 0)$ or $(0, \hat{y})$, (IVbc) $(\text{variable}, 0)$ or $(0, \hat{y})$, (IVca) $(0, 0)$ or $(0, \text{variable})$, (IVcb) $(\tilde{x}, 0)$ or $(0, \text{variable})$, and (IVcc) $(\text{variable}, 0)$ or $(0, \text{variable})$. When $b\beta/\alpha > 1/(s_2 - a)$, Domains IIa, IVaa, IVba, and IVca disappear (see Fig. 3). In similar ways, all Domains, but Ic, IIc, IIIa, and IVcc may disappear depending on parameter values.

Figure 6 demonstrates that the stable structure changes from coexistence to extinction as γ (the germination rate of triploid seed without

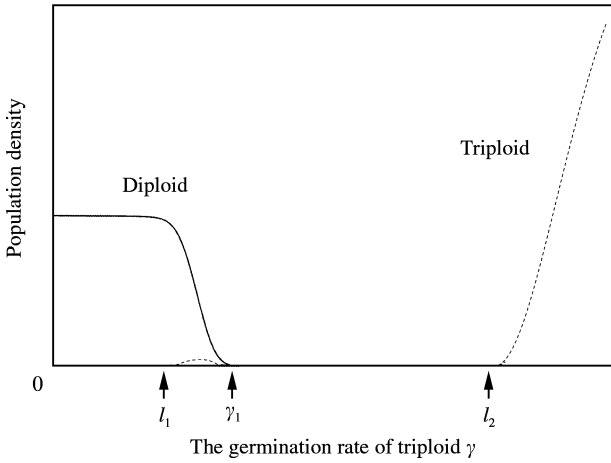


FIG. 6. Change in the equilibrium density of diploids and apomicts as γ increases from 0 to 1. $\alpha = 1.04$, $\beta = 2$, $\rho = 1$, $a = 1$, $b = 1$, $r = 0.8$, $s_1 = 2$, and $s_2 = 2$. (—) and (---) curves, respectively, indicate diploids and apomicts.

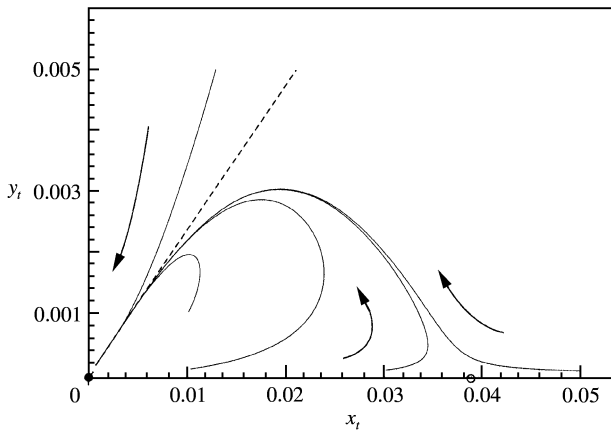


FIG. 7. The five trajectories of (x_t, y_t) for $\gamma = 0.676$, α , β , and ρ are the same as in Fig. 6. Each initial value is $(x_0, y_0) = (1, 1)$, $(0.01, 10^{-3})$, $(0.01, 10^{-4})$, $(0.03, 10^{-4})$, $(0.1, 10^{-4})$. Each (—) curve presents the trajectory with each initial value. The (○) and (●) circles are unstable and stable equilibria, respectively. The slope of the broken line indicates ψ^* and the ratio x_t/y_t monotonically approaches ψ^* .

crossing) increases. When $\gamma < l_1$, x_t converges to a positive equilibrium and y_t converges to 0. In other words, the population becomes purely diploid. When $l_1 < \gamma < \gamma_1$, diploids and triploids coexist. However, as γ increases to γ_1 , \hat{x} monotonically decreases, \hat{y} initially increases and subsequently decreases, and finally \hat{x} and \hat{y} approach 0, as γ increases from l_1 to γ_1 . If $\gamma_1 < \gamma < l_2$, both diploids and triploids become extinct. Figure 7 shows the trajectories of x_t and y_t for $\gamma_1 < \gamma < l_2$.

Here, \hat{y} (apomict) initially increases then decreases with increasing γ , as shown in Fig. 6. Thus, increasing γ does not always support the triploid population. If the germination rate of triploid seed asexually produced by triploid apomict γ is sufficiently small, most triploids are reproduced by crossing. Under these conditions, diploids and triploids coexist. As γ increases, diploids and apomicts are affected by the density effect of the seedlings. The number of triploids offspring increases with γ . Diploids are fertilized by triploids and become extinct. Subsequently, triploids also become extinct. When γ is sufficiently large, diploids become extinct. Under these conditions, the stability of the equilibrium depends of γ .

Figure 8 shows the trajectories of x_t and y_t for Domain (IVab) in Fig. 3. Whether diploids persist depends on the initial conditions. Both diploids and apomicts become extinct when $x_0/y_0 < \psi^*$ (shown by the dotted line); however, diploids can invade when $x_0/y_0 > \psi^*$. For example, a small number of diploids invade at a trivial equilibrium $(0, 0)$ and $x_0/y_0 > \psi^*$ and therefore the system moves to the other equilibrium $(\tilde{x}, 0)$. We compile the dynamics of this system as follows: (i) both diploids and apomicts become extinct (Domains Ia, IIa, IIIa, and IVaa), (ii) both diploids and apomicts coexist (Domains

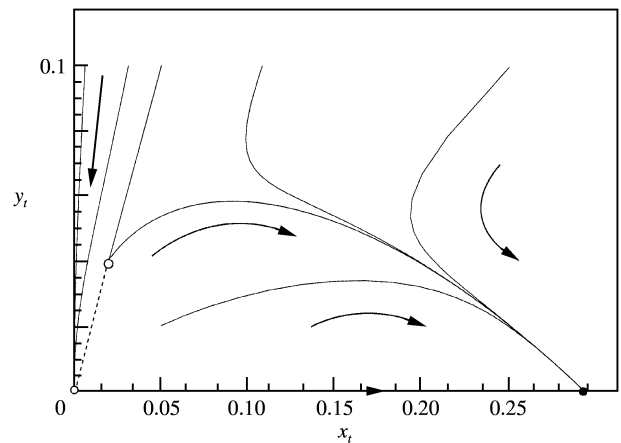


FIG. 8. The six trajectories of (x_t, y_t) for $\alpha = 1.6$, $\beta = 1$, $\gamma = 0.9$, $\rho = 1$, $a = 1$, $b = 1$, $r = 0.5$, $s_1 = 2$, and $s_2 = 2$. Each initial value is $(x_0, y_0) = (1, 1)$, $(1, 2)$, $(0.1, 1)$, $(0.05, 0.15)$, $(0.05, 0.02)$, $(0.25, 0.1)$. The (○) and (●) circles are unstable and locally stable equilibria, respectively. The slope of the (---) line indicates ψ^* .

IIIb, IIIc), (iii) only diploids can invade (Domains IIb, IIc, IVab, and IVac), (iv) only apomicts can invade (Domains Ib, Ic, IVab, and IVca), and (v) whether diploids or apomicts invade depends on the initial relative density (Domains IVbb, IVbc, IVcb, and IVcc).

4. Discussion

Based on our results, the coexistence of triploid apomicts and diploid sexuals does not require niche separation. However, coexistence is only possible under specific conditions, where both α (the germination rate of sexual diploid seeds) and γ (that of triploid seeds without crossing) are sufficiently small, as in Fig. 4. When diploids and apomicts coexist, the system has three equilibrium states: stable or periodic cycles or a chaotic state. These complex dynamics depend on a Ricker form density dependence. If the functional form of density dependence conforms to Michaelis–Menten [$F_i(z) = \varepsilon_i z / (m + z)$ in eqn (4)], this system always has a stable equilibrium. The coexistence conditions shown in Fig. 3 are the same irrespective of the functional forms of density dependence. System (5–7) is bistable in conditions (IVbb), (IVbc), (IVcb), and (IVcc). In these cases, neither apomicts nor diploids invade each other's population. Apomicts cannot increase where diploids already exist. Diploids cannot increase where apomicts already exist. This situation is thought to be unlikely in nature. In *Taraxacum*, which is perennial and has both sexual diploids and apomictic triploids, the latter have invaded broad areas in Japan where the native species is exclusively diploid (Morita *et al.*, 1990b; Ogawa & Isao, 1991). If the germination rate of triploids is large, a pure triploid population would be generated as in Case (I). In contrast, if the germination rate of diploids is large, they would make a pure diploid population as in Case (II).

The maintenance of sexual diploids depends on the difference between the germination rates of diploids and apomicts, $\alpha - \gamma$. If apomicts do not produce pollen, that is $b = 0$, $s_1 = s_2$, and $\alpha = \gamma$, then the slope of l_1 is smaller than 1, and diploids never persist. Coexistence of diploid and apomict is possible if apomicts produce pollen. If $b = 0$, both lines l_1 and l_2 in eqns (12) and (13)

pass on (0, 0) and Domain (III) in Fig. 3 vanishes. Facultative apomicts may be forced to pay the cost of pollen production when the germination rate of triploid apomicts is very low. When apomicts produce more pollen (b becomes large), diploids and apomicts may coexist, because Domain (III) becomes larger. Apomicts become extinct when diploids produce more pollen (a becomes large). Diploids become extinct when they produce less pollen (a becomes small).

The population structure depends on the germination rates of diploids and triploids (α and γ , respectively). However, we have little quantitative information on the germination rate or the numbers of seedlings produced by diploids and triploids. The germination rate of diploids depends on density, climate, and pollinator conditions, since diploids are considerably self-incompatible. If the population density is very low, the germination rate of diploids may be lower. Thus, the germination rate differs among habitats and between diploids and triploids owing to ecological conditions.

Crossing can alter genetic variability, but our model did not include this phenomenon. Crossing may also provide variability in agamosperms by promoting recombination (Mogie, 1992). Populations in the wild may be subject to immigration, since vectors such as birds can transport seeds over considerable distances. Isozyme evidence suggests that genetic variation exists between sexual and agamospermous species (Yahara *et al.*, 1991; Overath & Hamrick, 1998). Variation in agamospermy may be the result of crossing, immigration, or mutation. Spatial structure and genetic diversity should also be considered. Further modifications of our mathematical model are expected to contribute to the examination of the evolution of facultative agamosperms.

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REFERENCES

- ASKER, S. & JERLING, L. (1992). *Apomixis in Plants*. Boca Raton, FL: CRC Press.
- BAYER, R. J., PURDY, B. G. & LEBEDYK, D. G. (1991). Niche differentiation among eight sexual species of *Antennaria gaertner* (Asteraceae: Inuleae) and *A. rosea*, their allopolyploid derivative. *Evol Trends Plants* **5**, 109–123.
- CAMPBELL, C. S. & DICKINSON, T. A. (1990). Apomixis, patterns of morphological variation, and species concepts in subf. Maloideae (Rosaceae). *Syst. Bot.* **15**, 124–135.
- DEN NIJS, J. C. M. & STERK, A. A. (1984). Cytogeography of *Taraxacum* sectio *Taraxacum* and sectio *Alpestris* in France and adjacent parts of Italy and Switzerland, including some taxonomic remarks. *Acta. Bot. Neerl.* **33**, 1–24.
- DEN NIJS, J. C. M., KIRSCHNER, J., STEPANEK, J. & HULST, V. D. (1990). Distribution of diploid sexual plants of *Taraxacum* sect. *Ruderalia* in East-Central Europe, with special reference to Czechoslovakia *Plant Syst. Evol.* **170**, 71–84.
- DONCASTER, C. P., POUND, G. E. & COX, S. J. (2000). The ecological cost of sex. *Nature* **404**, 281–285.
- KAWAHARA, T., YAHARA, T. & WATANABE, K. (1989). Distribution of sexual and agamosperous populations of *Eupatorium* (Compositae) in Asia. *Plant Species Biol.* **4**, 37–46.
- KERSZBERG, M. (2000). The survival of slow reproducers. *J. theor. Biol.* **206**, 81–89.
- MAYNARD SMITH, J. (1978). *The Evolution of Sex*. Cambridge: Cambridge University Press.
- MOGIE, M. (1992). *The Evolution of Asexual Reproduction in Plants*. London, U.K.: Chapman & Hall.
- MOONEY, D. & SWIFT, R. (1999). *A Course in Mathematical Modeling*. Washington, DC: Mathematical Association of America.
- MORITA, T., STERK, A. A. & DEN NIJS, J. C. M. (1990a). The significance of agamosperous triploid pollen donors in the sexual relationships between diploid and triploid in *Taraxacum* (Compositae). *Plant Species Biol.* **5**, 167–176.
- MORITA, T., MENKEN, S. B. J. & STERK, A. A. (1990b). Hybridization between European and Asian dandelions (*Taraxacum* section *Ruderalia* and section *Mongolica*). 1. Crossability and breakdown of self-incompatibility. *New Phytol.* **114**, 519–529.
- OGAWA, K. & ISAO, M. (1991). Land-use selection by dandelions in the Tokyo metropolitan area, Japan. *Ecol. Res.* **6**, 233–246.
- OVERATH, R. D. & Hamrick, J. L. (1998). Allozyme diversity in *Amelanchier arborea* and *A. laevis* (Rosaceae). *Rhodora* **903**, 276–292.
- RICHARDS, A. J. (1973). The origin of *Taraxacum* agamospecies. *Bot. J. Linn. Soc.* **66**, 189–211.
- RICHARDS, A. J. (1986). *Plant Breeding System*. London, U.K.: Allen & Unwin.
- RICKER, W. (1954). Stock and recruitment. *J. Fish. Res. Board Can.* **11**, 559–623.
- SULLIVAN, V. I. (1976). Diploidy, polyploidy, and agamospermy among species of *Eupatorium* (Compositae). *Can. J. Bot.* **54**, 2907–2917.
- WILLIAMS, G. C. (1975). *Sex and Evolution*. Princeton, NJ: Princeton University Press.
- YAHARA, T., ITO, M., WATANABE, K. & CRAWFORD, D. J. (1991). Very low genetic heterozygosities in sexual and agamosperous populations of *Eupatorium altissimum* (Asteraceae). *Am. J. Bot.* **78**, 706–710.